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ESTIMATING SURVIVAL RATES FROM BANDING OF ADULT AND JUVENILE BIRDS

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Abstract: The restrictive assumptions required by most available methods for estimating survival probabilities render them unsuitable for analyzing real banding data. A model is proposed which allows survival rates and recovery rates to vary with the calendar year, and also allows juveniles to have rates different from adults. In addition to survival rates and recovery rates, the differential vulnerability factors of juveniles relative to adults are estimated. Minimum values of the variances of the estimators are also given. The new procedure is applied to sets of duck and goose data in which reasonably large numbers of adult and juvenile birds were banded. The results are shown to be generally comparable to those procured by other methods, but, in addition, insight into the extent of annual variation is gained. Combining data from adults and juveniles also increases the effective sample size, since the juveniles are assumed to enter the adult age class after surviving their initial year.

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The proper management of a wildlife species requires insight into the population dynamics of that species. The rate at which a population acquires new members (recruitment rate) and the rate at which members of a population die (mortality rate) are typically the most vital characteristics of the species' dynamics, although rates of immigration and emigration may be critical for certain populations. Generally, however, greatest attention is focused upon the annual mortality rate or, equivalently, its complement, the annual survival rate. For a game species this is the parameter over which the manager may have some control. It is difficult to induce an organism to reproduce at a higher rate or to emigrate from one population to another, but its probability of dying can be affected by modifying the regulations controlling the hunting: varying the daily or seasonal bag limit, altering the length of the open season or the timing of it, or selectively encouraging or discouraging the hunting of a particular species.

The problem which confronts the decision-maker, however, is determining mortality (or survival) rates for wild populations, so that any changes in them resulting from a modification of the regulations can be detected. Most of the methods which have been used in the past to estimate survival employ models which are not realistic for a limited population. Seber (1972) summarizes techniques which have been used to estimate survival from banding data and Anderson (1972) provides an extensive bibliography relating to banding analysis. Although assumptions are often not clearly stated, most models require survival probabilities to be constant from one year to another, which is unlikely to be true if hunting pressure or natural mortality factors vary. Generally, models do not allow juveniles to have survival rates different from adults, as is ordinarily the case. Nearly all models require recovery rates (rates of shooting and reporting of wild birds banded prior to the hunting season; *see* Anderson and Henny 1972:19) to be constant from one year to another. Again, this assumption is not likely to be met in practice. A more realistic model was recently proposed by Seber (1970), who allows survival rates and recovery rates to vary year to year. His method is specific to adult banding, however, and does not incorporate the bandings of young birds.

A need still exists for a model which provides a realistic representation of the data, yet which allows efficient estimates to be obtained. A single model will not prove optimal under all circumstances, however. If a species survives at a constant rate, for example, it is injudicious to estimate survival rates on a yearly basis. The method most appropriate for a particular body of data depends upon the set of assumptions deemed most plausible for those data. The most general model will not give reliable estimates unless the quantity of data is abundant, because such a model will include numerous parameters so that the amount of information about each parameter conveyed by the data in the sample will be small. Thus, the estimates are liable to be imprecise. A more restrictive model, on the other hand, employs fewer parameters, so each will be measured with greater precision. Better estimators ordinarily result from additional assumptions being made, provided the assumptions are valid.

A method is proposed here which is sufficiently general to apply under a wide variety of circumstances; yet, it is parsimonious in that no parameters are superfluous, i.e., survival of a hunted species is unlikely to be adequately represented by a model containing fewer parameters. We will allow the probability of adult survival from year i to year $(i + 1)$ to vary with the calendar year: S_i = Pr {adult bird alive at beginning of $(i + 1)$st year given it was alive at beginning of ith year}. We will also allow the recovery rate P_i to vary with the calendar year (or hunting season): P_i = Pr {adult bird is shot in ith year and reported then}. Notice that the recovery rate is a composite of the hunting mortality rate and the reporting rate.

We may include the banding of juvenile (here used to denote birds less than 1 year of age) as well as adult birds in the model. The following two restrictions, however, will be imposed: (1) In their 1st year, juveniles will be subjected to hunting mortality and reporting at an inflated (or deflated) rate $H \times P_i$ compared to the adult rate P_i. They will survive their 1st year at a fraction $D \times S_i$ of the adult rate S_i. H will represent the disproportionate vulnerability of juveniles to hunting mortality if adults and juveniles are reported at the same rate. D represents differential survival during their 1st year. We assume H and D do not change from one year to another; (2) Within any particular year all birds 1 year of age or older survive and are recovered at the same rate. Thus, 2nd-year birds are considered to be adult, and suffer mortality at the same rate as older birds.

I am grateful to R. L. Jessen for permission to use unpublished data from mallard (*Anas platyrhynchos*) bandings conducted by the Minnesota Department of Natural Resources. Other mallard bandings used in Example 1 were conducted by personnel of the Rice Lake, Agassiz, and Tamarac National Wildlife Refuges and the Northern Prairie Wildlife Research Center. I profited from discussions with H. W. Miller and, especially, L. M. Cowardin. D. R. Anderson made several valuable criticisms of an early draft of the manuscript, and P. F. Springer provided editorial assistance.

DERIVATION OF THE MODEL

We will consider the case where banding occurs in I consecutive years and recoveries are recorded for J years $(I \leq J)$. Assume a total of N_i adults are banded at the beginning of the ith year (prior to ith year hunting season). Of these a portion, N_iP_i, will be shot and reported in the ith year. A portion, N_iS_i, will survive the ith year

Table 1. Expected recoveries of birds banded as adults.

Year	Number banded	Expected number of recoveries in year 1	2	3	…	i	…	J	Not recovered
1	N_1	N_1P_1	$N_1P_2S_1$	$N_1P_3S_1S_2$	…	$N_1P_iS_1 \ldots S_{i-1}$	…	$N_1P_JS_1 \ldots S_{J-1}$	N_1W_1
2	N_2		N_2P_2	$N_2P_3S_2$	…	$N_2P_iS_2 \ldots S_{i-1}$	…	$N_2P_JS_2 \ldots S_{J-1}$	N_2W_2
⋮	⋮					⋮		⋮	⋮
i	N_i					N_iP_i	…	$N_iP_JS_i \ldots S_{J-1}$	N_iW_i

and enter the $(i+1)$st year. A fraction of these, $N_iS_iP_{i+1}$, will be shot and reported during the $(i+1)$st year, and so forth through the last year of recoveries, year J. A certain number of banded birds will not be recovered by the end of the Jth year. Let N_iW_i denote the expected value of this number. Then

$$W_i = 1 - P_i - P_{i+1}S_i - P_{i+2}S_iS_{i+1} - \cdots - P_JS_i \cdots S_{J-1}. \quad (1)$$

This procedure generates one line in a table of expected recoveries for each year in which banding occurs. Table 1 illustrates such a table.

Let A_{ij} be the actual number of adult birds banded in year i and recovered in year j, and let $A_{i\cdot}$ be the number of birds banded in year i and not recovered by the end of year J. Then $A_{i\cdot} = N_i - A_{ii} - A_{i,i+1} - A_{i,i+2} - \cdots - A_{iJ}$.

Thus, each of the birds banded in the ith year belongs to exactly one of the $(J-i+2)$ mutually exclusive and exhaustive classes: recovered in year i, recovered in year $i+1$, $\cdots$, recovered in year l, $\cdots$, recovered in year J, not recovered by Jth year.

Hence, the bandings form a multinomial experiment with cell expectations given in the ith line of Table 1. The probability function of the ith year's banding is $\Pr\{A_{ii}; A_{i,i+1}; \cdots; A_{iJ}; A_{i\cdot}\} = C_iP_i^{A_{ii}}(P_{i+1}S_i)^{A_{i,i+1}} \cdots (P_JS_i \cdots S_{J-1})^{A_{iJ}}W_i^{A_{i\cdot}}$, where $C_i = N_i!/(A_{ii}!A_{i,i+1}! \cdots A_{iJ}!A_{i\cdot}!)$ is a constant, i.e., C_i does not depend upon the values of the parameters.

An analogous model can be constructed to represent the bandings and recoveries of juvenile birds. Assume a total of M_i juveniles are banded in the ith year. If these were adult birds, the expected number of them recovered in the ith year would be M_iP_i. However, we allow for a differential vulnerability to hunting of juveniles to adults so that M_iHP_i is the expected number of direct recoveries. Of the M_i birds banded, a portion (M_iDS_i) are expected to survive into the $(i+1)$st year, where D is a differential vulnerability factor for 1st year survival. Those which do survive their initial year will function just as adults, and so a fraction, $P_{i+1}M_iDS_i$, of them will be recovered in year $(i+1)$. These considerations lead to a table of expected recoveries of birds banded as juveniles, analogous to Table 1. V_i, the probability that a bird banded as a juvenile in year i will not be recovered by the end of year J, is given by

$$\begin{aligned} V_i &= 1 - HP_i - DP_{i+1}S_i - DP_{i+2}S_iS_{i+1} - \cdots - DP_JS_i \cdots S_{J-1} \\ &= 1 - (H-D)P_i - D(1-W_i) \end{aligned}$$

in terms of W_i as defined by Equation 1.

Let B_{ij} be the number of juvenile birds banded in year i and recovered in year j, and let $B_{i\cdot}$ be the number not recovered by the end of the Jth year. The probability function of the ith year's banding of juveniles is

$$Pr\{B_{i.}\} = C'_i(HP_i)^{B_{ii}}(DP_{i+1}S_i)^{B_{i,i+1}} \cdots (DP_JS_i \cdots S_{J-1})^{B_{iJ}}V_i^{B_i},$$

where

$$C'_i = M_i!/(B_{ii}!\,B_{i,i+1}! \cdots B_{iJ}!\,B_i!)$$

is another constant.

Making the usual assumption that each banded individual is or is not recovered independently of each other individual leads to a model incorporating the bandings and recoveries for both adults and juveniles in all years. The joint probability function is simply the product of each individual probability function:

$$\begin{aligned} Pr\{A_{ij}, B_{ij}\} &= \prod_{i=1}^{I} Pr\{A_{ij}\}\,Pr\{B_{ij}\} \\ &= \prod_{i=1}^{I}\Big[C_iC'_iH^{B_{ii}}P_i^{(A_{ii}+B_{ii})}\prod_{j=i+1}^{J}D^{B_{ij}} \\ &\quad\times\Big(P_j\prod_{m=i}^{j-1}S_m\Big)^{(A_{ij}+B_{ij})}W_i^{A_i}V_i^{B_i}\Big]. \quad (2)\end{aligned}$$

ESTIMATION OF THE PARAMETERS

With bandings in years 1 through I, we may estimate recovery rates for each of those years. Survival probabilities can be calculated for each but the last year. Including the differential vulnerability factors, the following quantities are estimable: H; D; $P_1, P_2, \cdots, P_I$; $S_1, S_2, \cdots, S_{I-1}$.

If recoveries are available from years beyond the last year of banding, i.e., if $J > I$, certain parameters enter the probability function (Equation 2) but cannot be directly estimated. These parameters are $P_{I+1}, P_{I+2}, \cdots, P_J$; $S_I, S_{I+1}, \cdots, S_{J-1}$. The quantity

$$\theta = P_{I+1}S_I + P_{I+2}S_IS_{I+1} + \cdots + P_JS_IS_{I+1} \cdots S_{J-1}$$

can, however, be estimated. This quantity is not ordinarily useful unless further assumptions are made, either about the recovery rates or the survival rates, but estimation of the parameters of interest requires that θ be estimated.

Maximum likelihood estimators (e.g., Kendall and Stuart 1967:35ff) of the parameters were obtained from Equation 2. These estimators are the values of the parameters which would most likely result in the data which were actually observed.

The differential vulnerability of juveniles to hunting is estimated by Equation 3. Each term in the denominator is the expected number of direct (1st-year) recoveries of juveniles if their 1st-year recovery rate were identical to that of adult birds. Each term in the numerator is the actual number of juvenile direct recoveries. The ratio then is a measure of the excess vulnerability of juveniles in their 1st year as compared to adults.

$$\hat{H} = \sum_{i=1}^{I} B_{ii} \Big/ \sum_{i=1}^{I} M_i\hat{P}_i \qquad (3)$$

The differential survival of juveniles is estimated by Equation 4. Here $1 - \hat{W}_i$ estimates the proportion of adults banded in year i which are recovered by the end of year J, so $1 - \hat{W}_i - \hat{P}_i$ estimates the proportion recovered in some year beyond the year of banding. Hence, each term in the denominator represents the number of indirect recoveries of juveniles expected if they were adults. In the numerator, each term $\sum_{j=i+1}^{J} B_{ij}$ indicates the actual number of indirect recoveries of juveniles. Since we assumed juveniles function as adults once they attain the age of 1 year, any discrepancy between the numerator and denominator reflects differential survival in the juveniles' 1st year.

$$\hat{D} = \frac{\sum_{i=1}^{I}\sum_{j=i+1}^{J} B_{ij}}{\sum_{i=1}^{I} M_i(1 - \hat{W}_i - \hat{P}_i)} \qquad (4)$$

In the Equation 5 for $\hat{P}_1$, the denominator estimates the number of banded birds (adult and juvenile adjusted for differential vulnerability) that are ob[illegible] in year k, regardless of the year in which they were banded. The numerator is the number of recoveries in the kth year from all bandings; hence, the ratio indicates the recovery rate in the kth year.

$$\hat{P}_k = \sum_{i=1}^{k}(A_{ik}+B_{ik}) \times \Big[\sum_{i=1}^{k-1}(N_i+\hat{D}M_i)\prod_{m=i}^{k-1}\hat{S}_m + (N_k+\hat{H}M_k)\Big]^{-1} \qquad (5)$$

The survival rate for year k is estimated by Equation 6. The denominator estimates the expected number of banded birds that would be recovered in all years beyond the kth if they had all survived the kth year, i.e., if $S_k = 1$. The numerator expresses the actual number of recoveries, so their ratio estimates the proportion surviving the kth year, i.e., S_k.

$$\hat{S}_k = \sum_{i=1}^{k}\sum_{j=k+1}^{l}(A_{ij}+B_{ij}) \times \Big[\sum_{i=1}^{k}(N_i+\hat{D}M_i)\Big(\sum_{j=k}^{l-1}\hat{P}_{j+1}\prod_{\substack{m=i\\m\neq k}}^{j}\hat{S}_m + \hat{\theta}\prod_{\substack{m=i\\m\neq k}}^{l-1}\hat{S}_m\Big)\Big]^{-1} \qquad (6)$$

In (6), θ can be estimated by

$$\hat{\theta} = \frac{\sum_{i=1}^{l}\sum_{j=l+1}^{l}(A_{ij}+B_{ij})}{\sum_{i=1}^{l}(N_i+\hat{D}M_i)\prod_{m=i}^{l-1}\hat{S}_m}$$

The W_i in (4) are given by (1) and are estimated by $\hat{W}_i = A_i/N_i$.

Solution of the Equations

Each of the estimating equations involves the parameters implicitly, and no direct solutions have been obtained; however, simple iterative methods can be applied to provide solutions with relative ease.

If initial estimates of $\{P_k\}$ and $\{S_k\}$ are provided, a straightforward iterative procedure is to calculate $\hat{H}$ and $\hat{D}$ based upon $\{\hat{P}_k\}$. Then new values of $\{\hat{P}_k\}$ are calculated by using Equation 5 with the values of $\hat{H}$ and $\hat{D}$ just computed. Then new estimates $\{\hat{S}_k\}$ are obtained by using Equation 6 with $\hat{D}$ and $\{\hat{P}_k\}$. This sequence is then repeated (iterated) until the estimates converge to their final values. The initial estimates need not be accurate, and the examples considered thus far have not required an excessive number of iterations. A FORTRAN IV computer program that carries out the estimation procedure is available from the author.

Table 2. Recoveries of female mallards banded in Minnesota 1967–1970.[a]

Adults

Year	Number banded	Number of recoveries in year 1967	1968	1969	1970	Not recovered
1967	637	62	16	11	4	544
1968	338		16	9	5	308
1969	67			6	5	56
1970	93				12	81

Locals (flightless young)

Year	Number banded	Number of recoveries in year 1967	1968	1969	1970	Not recovered
1967	298	40	4	2	5	247
1968	288		31	9	2	246
1969	494			33	12	447
1970	538				81	457

[a] Data from Minnesota Department of Natural Resources and U. S. Bureau of Sport Fisheries and Wildlife.

Estimates of the Variances

The theory of maximum likelihood estimation (e.g., Kendall and Stuart 1967:55) can be applied to determine the asymptotic distribution of the estimators. The estimators are consistent; i.e., as the sample sizes increase, the estimators tend to the

Table 3. Estimates of parameters for female mallards banded in Minnesota.

Year	Survival rate	Recovery rate (P_t)[a]	Direct recovery rate (R_t)
1967	0.48 (0.091)[b]	0.071 (0.0091)	0.066 (0.0100)
1968	0.57 (0.141)	0.058 (0.0089)	0.047 (0.0115)
1969	0.40 (0.123)	0.070 (0.0100)	0.090 (0.0350)
1970		0.100 (0.0170)	0.121 (0.0350)

[a] As defined in the text.
[b] Standard errors are in parentheses.

true values of the parameters. Moreover, the asymptotic distribution of the estimators is normal, with the true parameter values as means and a variance-covariance matrix Λ. Λ is formed by inverting the matrix of second partial derivatives of the likelihood function, taking expectations, and changing the sign of each element. Although this can be done for any particular case, extensive computations are required; no simple formulas have been found for the general case. However, useful lower bounds for the variances are readily calculated (Wilks 1962:377; Tiao and Guttman 1964). These arise by considering one estimator at a time, and assuming the other parameters are fixed. These are given by:

$$\mathrm{Var}(\hat{H}) > \hat{H}^2 \Big/ \sum_{i=1}^{t} B_{ii}$$

$$\mathrm{Var}(\hat{D}) > \hat{D}^2 \Big/ \sum_{i=1}^{t} \sum_{j=i+1}^{t} B_{ij}$$

$$\mathrm{Var}(\hat{P}_k) > \hat{P}_k^2 \Big/ \sum_{i=1}^{k} (A_{ik} + B_{ik}).$$

$$\mathrm{Var}(\hat{S}_k) > \hat{S}_k^2 \Big/ \sum_{i=1}^{k} \sum_{j=k+1}^{t} (A_{ij} + B_{ij}).$$

Note that each value is simply the square of the estimator divided by the number of observations entering into the numerator of the estimator.

EXAMPLES

Example 1.—Table 2 displays the numbers of mallards banded in Minnesota in the years 1967 to 1970 and recovered by 1970. Adult females and local (flightless young) females are included. All bandings were done by the Minnesota Department of Natural Resources and the U.S. Bureau of Sport Fisheries and Wildlife prior to each hunting season.

Estimates of the parameters together with their standard errors, calculated from the asymptotic variance-covariance matrix, are given in Table 3. Also shown are the direct recovery rates of adults ($R_i = A_{ii}/N_i$) with their standard errors ($\sqrt{R_i(1-R_i)/(N_i-1)}$). Note that each recovery rate $\hat{P}_i$ has a standard error appreciably smaller than that of the corresponding direct recovery rate. This increase in precision results from the rates $\{\hat{P}_i\}$ being efficient, using recoveries from the bandings of all years (adjusted for survival) and both age classes (adjusted for differential vulnerability), while R_i is based only upon recoveries from the adult birds banded in the ith year. The increased recovery rate in 1970 corresponds with a liberalization of the mallard bag limit in Minnesota from one daily (two in possession) in 1969 to four daily (eight in possession) in 1970. It will be necessary to analyze 1971 recoveries when they become available in order to determine S_4 and thereby ascertain the effect of liberalization of the bag limit on survival rates.

Local mallards suffered hunting mortality in their 1st year at a rate 55 percent higher than adults, as indicated by $\hat{H} = 1.55$ (95 percent confidence limits of 1.10, 2.00).

Table 4. Estimated survival rates and recovery rates for western Canada goose.

Year	Survival rate	Recovery rate
1950	0.70	0.037
1951	0.53	0.084
1952	0.82	0.131
1953	0.43	0.051
1954	0.72	0.086
1955	0.62	0.114
1956	0.64	0.094
1957	0.82	0.044
1958	0.84	0.094
1959	0.61	0.068
1960	0.29	0.080
1961	0.73	0.130
1962	0.65	0.072
1963	0.53	0.056
1964	0.76	0.090
1965		0.093
Average	0.65	0.084

On the average, they survived their initial year at only 38 percent of the adult rate, since $\dot{D} = 0.38$ (0.24, 0.52).

Example 2.—Hanson and Eberhardt (1971) provide an example with a long series of consecutive years' bandings and recoveries. They examined the Columbia River, Washington population of the western Canada goose (*Branta canadensis*). Banding occurred in each year from 1950 to 1967 with the exception of 1966. To exemplify the method, I considered bandings between 1950 and 1965 together with *all recoveries through the 1967 hunting season*. To conserve space, the recovery tables are not repeated here (*see* Tables 19–22 of Hanson and Eberhardt).

The estimated survival rates and recovery rates are given in Table 4. Note the considerable variation in annual survival rates, conflicting with the assumption made implicitly by Hanson and Eberhardt that adult survival is constant. The simple average of the survival estimates is $S = 0.65$, a figure which lies between two estimates made by Hanson and Eberhardt: $S = 0.60$, based on indirect recoveries of birds banded as juveniles; and $S = 0.685$, based upon birds banded as adults.

Hanson and Eberhardt (1971) noted that juveniles suffered lower hunting mortality than adults did, and this is borne out by a differential vulnerability to hunting of less than one, $\dot{H} = 0.72$. Since $\dot{D} = 1.18$, we infer that juveniles typically survived at a rate higher than adults, which seems reasonable in light of their reduced susceptibility to hunting. However, Hanson and Eberhardt, upon comparing the adult survival rates of 0.60 (based on birds banded as juveniles) and 0.685 (based on birds banded as adults), assert that mortality is higher *among young birds*.

Table 5. Expected recovery tables for hypothetical example.

Adults

Year	Number banded	Number of recoveries in year: 1	2	3	Not recovered
1	60	6	3	1	50
2	75		9	4	62
3	50			4	46

Juveniles

Year	Number banded	Number of recoveries in year: 1	2	3	Not recovered
1	175	26	5	2	142
2	200		36	7	157
3	150			18	132

DISCUSSION

In summary, this new procedure offers three advantages over most existing models: (1) Survival rates and recovery rates may vary with the calendar year. This feature is particularly important for populations which are hunted under varying sets of regulations; (2) Bandings of juvenile as well as adult birds are accommodated in one model, increasing the effective sample size and imparting more precision to the estimators; (3) Variance estimates can be obtained, although with considerable difficulty, as was done in Example 1. Moreover, lower bounds for the variances can be readily calculated.

The usefulness of these lower bounds in designing a banding program can be demonstrated by a hypothetical example. Suppose it is possible to band, prior to the hunting season of each year, 50–75 adult birds and 150–200 juvenile birds. Three years of banding are envisioned. What sort of precision is to be expected in the estimates of survival?

Assume survival rates of 40 percent one year and 70 percent the next, recovery rates of 10, 12, and 8 percent, and differential vulnerability factors of $H = 1.50$ and $D = 0.6$. The following analysis is not sensitive to the values of these parameters. These are typical values which were chosen to illustrate the method. Recovery tables as indicated in Table 5 would then be expected to result. The minimum possible values of the variances can be calculated as the square of the parameter being estimated divided by the number of observations used in the estimate. For example, $\mathrm{Var}(\dot{S}_1) > S_1^2/(3 + 1 + 5 + 2) = 0.0145$. Similarly, $\mathrm{Var}(\dot{S}_2) > S_2^2/(1 + 4 + 2 + 7) = 0.0350$. *Minimal* 95 percent confidence intervals for these values are thus given by (0.16, 0.64) for $\dot{S}_1$ and (0.33, 1.07) for $\dot{S}_2$. Hence, after banding more than 700 birds, the resultant confidence intervals will be at least this wide. Careful consideration should be given to whether or not estimates that are this imprecise are worth the expense.

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